

# Successful and Unsuccessful Drilling Predation in Recent Pelecypods

by

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*Abstract.* A survey of 43 samples of empty Recent pelecypod valves from seven cold-temperate and 10 tropical shallow-water sites revealed an equatorward decrease in the incidence of complete gastropod drill holes. This result, which runs counter to earlier studies of drilling in turritellid gastropods, is consistent with the generalization that slow methods of predation (including drilling) decrease in importance toward the tropics because they place the predators at undue risk. Among naticid-drilled pelecypods, there is also an equatorward decrease in the incidence of incomplete drill holes.

Analysis of a sample of *Pseudocardium sachalinense* (Schrenck, 1862) from Hokkaido, Japan, suggests that incomplete holes usually represent unsuccessful drilling attacks. Because complete and incomplete holes in this sample were statistically indistinguishable with respect to both size and position, we were unable to identify specific shell features contributing to the high overall effectiveness of the shell of *P. sachalinense* as protection against drilling by naticids.

## INTRODUCTION

Drilling is a common form of predation on shell-bearing marine invertebrates. Using chemical and mechanical means, the predator (usually a gastropod or octopod) excavates a hole through the prey's shell wall. In most cases, a hole that completely penetrates through the shell indicates successful predation, whereas an incomplete drill hole, which does not reach the inner shell surface, generally indicates unsuccessful drilling. Although exceptions occur (see below), the distinction between complete and incomplete drill holes in a sample of "dead" shells makes it possible to infer predation success during the subjugation phase of a drilling predator's attack. This, in turn, makes drilling ideal for the study of geographical and temporal patterns in predation intensity.

Previous studies have generally pointed to the conclusion that drilling is ecologically and evolutionarily more important in the tropics than at higher latitudes. Tropical turritellid gastropods show higher frequencies of complete drill holes among empty shells than do temperate species (DUDLEY & VERMEIJ, 1978; ALLMON *et al.*, 1989). This

pattern parallels the equatorward increase in the diversity of drilling gastropods (MARINCOVICH, 1977; TAYLOR & TAYLOR, 1977). A latitudinal pattern in the distribution of incomplete drill holes, and therefore in the effectiveness of shell armor as a defense against drilling, might also be expected, because the expression of shell armor among mollusks generally increases from high to low latitudes (VERMEIJ, 1978, 1987). No evidence on this expectation has been published to date. However, most mobile mollusks seem to have adapted against drilling predators not through the development of thick armor, but by emphasizing attributes enabling the prey to avoid detection or to escape before being caught (VERMEIJ, 1978, 1987). Not only do many species show well-developed escape responses to drilling gastropods, but most drilling attempts by naticacean gastropods appear to be successful, judging from the low frequencies of incomplete holes in most prey species. High frequencies of incomplete holes (and therefore presumably of unsuccessful attacks during the subjugation phase) are reported mainly for the sedentary prey of muricacean drillers (ADEGOKE & TEVESZ, 1974; KOJUMDJIEVA, 1974; BLACK, 1978; VERMEIJ, 1980b, 1987; PALMER, 1982). If muriceans fail more often than do naticaceans in attempting to drill their prey, an equatorward increase in drilling-related armor might occur only among the prey of muricaceans.

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The evaluation of these ideas requires the analysis of systematically collected samples of empty shells from many geographical localities. In this paper, we report the results of surveys conducted by us during the last 12 yr on frequencies of complete and incomplete drilling in shallow-water pelecypods from various temperate and tropical localities. As will be seen, most of the generalizations that have been made about drilling are challenged by the new evidence.

## MATERIALS AND METHODS

The localities at which we surveyed empty pelecypod valves are listed in Table 1. At each site, all intact paired and unpaired valves were collected from the beach surface. We assumed that valve sorting by waves and shell collecting by beach-goers did not materially alter the incidence of complete and incomplete drill holes in the population. That these assumptions are valid is suggested by the fact that the observed frequencies of complete and incomplete drilling in paired valves were statistically indistinguishable from the respective frequencies in unpaired valves in all samples. Each shell in a sample was carefully scanned for the presence of complete and incomplete drill holes. Samples of all species are conserved in the Vermeij collection; a subsample of *Pseudocardium sachalinense* from Locality 2 has been deposited at the U.S. National Museum of Natural History in Washington.

The incidence of complete and incomplete drilling was calculated as the number of holes divided by the number of individuals. The number of individuals was taken as the number of valve pairs plus half the number of unpaired valves. Drilling was assessed only in intact valves. This restriction may lead to an overestimation of the importance of drilling as a cause of mortality because individuals dying as a result of shell breakage are excluded (VERMEIJ, 1980a), but it should not affect the calculation of drilling success (the number of incomplete drill holes divided by the total number of holes). The incidence of complete holes was assessed only in samples of 10 or more individuals; drilling success was calculated only in samples in which the total number of drill holes was 10 or more.

In order to determine whether and how complete drill holes differ from incomplete ones, we measured the outer diameter of each hole (that is, the diameter as seen on the shell's exterior) and calculated the position of each hole along the anteroposterior and dorsoventral axes of the valve. The anteroposterior position was calculated as the distance from the anterior edge of the shell to the anterior edge of the hole divided by the anteroposterior length of the shell along a line passing through the middle of the hole. Similarly, the dorsoventral position of the hole was calculated as the distance from the dorsal edge of the valve to the dorsal edge of the hole divided by the dorsoventral length of the shell along a line passing through the middle of the hole.

The identity of drilling predators was inferred from the

Table 1

Localities of samples of empty pelecypod valves.

Locality 1. Abashiri City, moderately exposed sand beach on Okhotsk Sea, north coast of Hokkaido, Japan, taken 14–16 July 1988, by G.J.V., E.C.D., and E.Z. Likely predator: <i>Natica (Tectonatica) janthostoma</i> (Deshayes, 1841).
Locality 2. Tsukushikoi, exposed sand beach at Cape Aikappu, southeastern Hokkaido, Japan, taken 21–31 July 1988, by G.J.V., E.C.D., and E.Z. Likely predator: <i>N. janthostoma</i> .
Locality 3. Akkeshi Bay, sheltered shore of cobble and sandy silt at Akkeshi Marine Biological Station, southeastern Hokkaido, Japan, taken 31 July and 1 August 1988, by G.J.V., E.C.D., and E.Z. Likely predators: <i>Ocenebra japonica</i> (Dunker, 1860) and <i>O. adunca</i> (Sowerby, 1834).
Locality 4. Outer part (Nakanose) of Akkeshi Bay, heavily bioeroded mudstone at depth of 4 m, the pelecypods in abandoned pholad holes, taken 20 July 1988, by G.J.V. and E.C.D. Likely predator: <i>Nucella freycineti</i> (Deshayes, 1841).
Locality 5. Cape Elizabeth, south of Portland, Maine, USA, tidepool at mid-tide level; taken 11 August 1988, by G.J.V. and E.Z. Predator: <i>Nucella lapillus</i> (Linnaeus, 1758).
Locality 6. Sheep Island, off Deer Isle, Maine, taken 24 August 1988, by E.C.D. Predator: <i>N. lapillus</i> .
Locality 7. Fay Beach, Vineyard Sound, Massachusetts, depth of 1.5 m on sand; taken 10 August 1988, by E.C.D. Likely predator: <i>Euspira heros</i> (Say, 1822).
Locality 8. Wom Village, west of Wewak, Papua New Guinea, sheltered sand beach; taken 23–24 June 1979, by G.J.V. and E.Z. Likely predators: various naticids, especially <i>Polinices (P.) tumidus</i> (Swainson, 1840).
Locality 9. Suva Point, Viti Levu, Fiji, mudflat; taken 23 March 1986, by G.J.V. Likely predators: various naticids.
Locality 10. El Playon, Bahía de Amuay, west coast of Paraguaná Peninsula, Venezuela, sand beach; taken 13–17 July 1977, by G.J.V. and E.Z. Likely predators: various naticids.
Locality 11. Las Lajas, Pacific coast of Chiriquí Province, Panama, exposed sand beach; taken 17–20 July 1978, by G.J.V. and E.Z. Likely predators: various naticids.
Locality 12. Playa Brava, Pacific coast of Veraguas Province, Panama, relatively sheltered sand beach; taken 21–25 August 1978, by G.J.V. and E.Z. Likely predators: various naticids.
Locality 13. Isla Naos, Pacific coast of Panama Province, Panama, sheltered sand beach; taken 7–26 February 1986, by G.J.V., E.C.D., and E.Z. Likely predators: various naticids.
Locality 14. Playa Vernado, Pacific coast of Panama Province, Panama, sheltered sand beach and mudflats; taken April to June 1976, by G.J.V. and E.Z. Likely predators: various naticids.
Locality 15. Playa Venado; taken July 1978, by G.J.V. and E.Z.
Locality 16. Playa Venado; taken February 1986, by G.J.V., E.C.D., and E.Z.
Locality 17. Punta Chame, Pacific coast of Panama Province, Panama, exposed sand beach; taken 9 February 1986, by G.J.V. and E.C.D. Likely predators: various naticids.

shapes of drill holes (see CARRIKER & YOCHELSON, 1968), from direct observations of predation, and from the co-occurrence of known drillers. Muricacean holes are nearly cylindrical and have an evenly rounded bottom if incomplete, whereas naticacean holes (Figure 1) are markedly tapered and have a slightly raised bottom when incomplete.



Figure 1

Incomplete drill hole, presumably made by the naticid *Natica janthostoma*, on a valve of *Pseudocardium sachalinense* from Locality 2 (Tsukushikoi, Hokkaido, Japan).

## RESULTS AND DISCUSSION

### Geographical Patterns in Complete Drilling

Drilling is an important cause of death in many pelecypod species. The survey in Table 2 shows that drilling frequencies exceeding 0.50 occur in 2 of 13 cold-temperate samples (15%) and in only 2 of 30 tropical samples (6.7%). Contrary to the situation in the gastropod family Turritellidae, in which an equatorward increase in drilling frequency was found (DUDLEY & VERMEIJ, 1978; ALLMON *et al.*, 1989), the data on pelecypods point to a poleward increase in drilling. A nonparametric comparison between the 30 tropical samples and the 13 cold-temperate samples of Table 2, together with drilling frequencies of four additional cold-water samples reported by SCHÄFER (1972) from the North Sea and by COMMITO (1982) from Maine, shows that the frequency of complete drilling is significantly lower in the tropics (median frequency 0.09) than in the cold-temperate areas (median frequency 0.24,  $P < 0.01$ , Mann-Whitney  $U$ -test).

Additional data in the literature suggest that our tropical samples were very similar to previously studied material from tropical sites with respect to the distribution of drilling frequencies. The median frequency of complete drilling in these samples from Guam (VERMEIJ, 1980a), Indonesia (VERMEIJ, 1980b), and Barbados (SANDER & LALLI, 1982) is 0.09, a value identical to that in the tropical samples of Table 2.

Only one study of drilling predation has been done in

the polar regions. AITKEN & RISK (1988) report drilling frequencies of 0.01 to 0.90 among four Recent shallow-water pelecypod species from Clyde River in the eastern Canadian Arctic. Late Pleistocene and Holocene samples of these and other species at other Arctic sites generally show drilling frequencies below 0.10; only 1 of 15 samples (6.7%) shows a frequency of complete drilling higher than 0.50. These frequencies are thus more like those in the tropics than the cold north temperate zone.

Two small surveys of warm-temperate pelecypod drilling have been published, one on seven species in Italy (VIGNALI & GALLEN, 1986) and one on three species in South Australia (LAWS & LAWS, 1972). Both surveys report high frequencies of drilling (median frequency 0.21) comparable to the high values reported here for cold-temperate samples. Other scattered reports on warm-temperate thin-shelled pelecypods in Japan (MUKAI, 1972), Ireland (NEGUS, 1975), and the eastern United States (FRANZ, 1977; ROSEWATER, 1980; WILTSE, 1980) similarly indicate high frequencies of complete drilling.

Like other forms of predation, drilling varies greatly in its intensity on a small spatial scale as well as over time at individual sites (VERMEIJ, 1980a; WILTSE, 1980; COMMITO, 1982). Geographical patterns must therefore be very strong if they are to be detected above the "noise" of local and short-term temporal variation. The limited data at hand, most of which come from the northern hemisphere, suggest that the highest frequencies of complete drilling occur at mid-latitudes, with lower frequencies being

Table 2

Incidence of complete (C) and incomplete (I) drilling (expressed as percentage of individuals) in empty pelecypod valves.

Species	Lc.	n	C	I	Eff.
<i>Mactra (M.) chinensis</i> (Philippi, 1846)	1	44.5	81%	16%	0.16
<i>Pseudocardium sachalinense</i> (Schrenck, 1862)	1	10.5	38%	9%	—
<i>Peronidia venulosa</i> (Schrenck, 1861)	1	11	45%	9%	—
<i>Pseudocardium sachalinense</i>	2	122	16%	25%	0.61
<i>Peronidia venulosa</i>	2	30.5	16%	33%	0.67
<i>Protothaca (Callithaca) adamsi</i> (Reeve, 1863)	3	87	26%	8%	0.23
<i>Clinocardium californiense</i> (Deshayes, 1839)	3	11	0	0	—
<i>Clinocardium uchidai</i> Habe, 1955	3	40	0	0	—
<i>Protothaca (Novathaca) euglypta</i> (Sowerby, 1914)	4	18	94%	6%	0.06
<i>Mytilus edulis</i> Linnaeus, 1758	5	56.5	26%	0	—
<i>Mytilus edulis</i>	6	37	14%	3%	—
<i>Spisula (Hemimactra) solidissima</i> (Dillwyn, 1817)	7	60	5%	2%	—
<i>Cochlodesma leanum</i> (Conrad, 1831)	7	13	23%	0	—
<i>Meretrix lusoria</i> (Röding, 1798)	8	35	9%	0	—
<i>Codakia (Ctena) bella</i> (Conrad, 1837)	9	22	9%	0	—
<i>Anadara inaequalis</i> (Linnaeus, 1758)	9	14	0	7%	—
<i>Mactra (Macrotoma) fragilis</i> (Gmelin, 1791)	10	11.5	0	0	—
<i>Pitar (P.) albida</i> (Gmelin, 1791)	10	18.5	22%	0	—
<i>Protothaca (Leukoma) granulata</i> (Gmelin, 1791)	10	20.5	29%	0	—
<i>Chione (C.) cancellata</i> (Linnaeus, 1767)	10	10	0	0	—
<i>Mactrellona exoleta</i> (Gray, 1847)	11	21.5	9%	2%	—
<i>Tivela (T.) byronensis</i> (Gray, 1838)	11	26	12%	0	—
<i>Tivela (Planitivela) planulata</i> (Broderip & Sowerby, 1830)	11	14.5	0	0	—
<i>Pitar (Hysteroconcha) lupanaria</i> (Lesson, 1830)	11	16.5	36%	0	—
<i>Pitar (H.) brevispinosus</i> (Sowerby, 1851)	11	12	25%	0	—
<i>Pitar (Lamelliconcha) unicolor</i> (Sowerby, 1835)	11	14	0	0	—
<i>Donax carinatus</i> Hanley, 1843	11	28	0	0	—
<i>Megapitaria squalida</i> (Sowerby, 1835)	12	11.5	43%	0	—
<i>Protothaca (Tropithaca) grata</i> (Say, 1831)	13	57	2%	4%	—
<i>Laevicardium (L.) elenense</i> (Sowerby, 1840)	13	15.5	0	0	—
<i>Donax gracilis</i> Hanley, 1845	13	19.5	13%	0	—
<i>Diplodonta subquadrata</i> (Carpenter, 1856)	13	39.5	17%	0	—
<i>Mactrellona exoleta</i>	14	16.5	16%	0	—
<i>Dosinia dunkeri</i> (Philippi, 1844)	14	19.5	36%	0	—
<i>Tellina (Eurytellina) laceridens</i> Hanley, 1844	14	23	4%	0	—
<i>Mactrellona exoleta</i>	15	11.5	0	0	—
<i>Tellina laceridens</i>	15	19	5%	0	—
<i>Tellina (Angulus) subtrigona</i> (Sowerby in Reeve, 1866)	15	10.5	0	0	—
<i>Temnoconcha cognata</i> C. B. Adams, 1852	15	28.5	7%	0	—
<i>Tagelus peruvianus</i> Pilsbry & Olsson, 1941	15	12	0	0	—
<i>Chione (Iliochione) subrugosa</i> (Wood, 1828)	16	29	78%	7%	0.09
<i>Protothaca (Leukoma) mcgintyi</i> Olsson, 1961	16	10.5	57%	10%	—
<i>Mactrellona exoleta</i>	17	18.5	5%	0	—

Key: Lc.—Locality. n—Number of individuals. C—Number of complete drill holes divided by n. I—Number of incomplete drill holes divided by n. Eff.—Effectiveness of armor: number of incomplete holes divided by total number of drill holes.

more typical of the tropical sites and the one polar area that have been studied to date.

Geographical patterns in drilling may result from systematic variations in the abundance of drilling predators, the abundance or effectiveness of other causes of mortality (especially those that remove shells from the sampled population), or artifacts of taxonomy whereby unusually susceptible groups happen to be well represented in certain geographical regions. We have no data on geographical patterns in the abundance of drilling predators. With respect to the second factor (removal of shells from the

sampled population), it may be noted that breakage is a common cause of death in tropical epifaunal and shallow-burrowing pelecypods (VERMEIJ, 1980a). The frequencies of complete drilling in Table 2 and in VERMEIJ (1980a) are therefore almost certainly overestimates for the tropical species, because we specifically eliminated broken valves from our survey. The apparent increase in the frequency of complete drilling from the tropics to the northern mid-latitudes may therefore be even greater than our data indicate. Exploitation of clams by humans may also eliminate valves from the population, and would similarly result in

an overestimate of observed frequencies of complete drilling. This is likely to be a problem chiefly in Panama, where several of the sampled species (especially the venerids *Chione subrugosa*, *Protothaca grata*, and *P. mcgintyi*) are commonly used for food. Although pelecypods are also widely harvested in Japan, the species surveyed by us are apparently not exploited.

Taxonomic artifacts may be investigated by assessing geographical patterns within families. Available data permit the study of only one family, the Mactridae. The six temperate mactrid samples in Table 2 and the literature (FRANZ, 1977; VIGNALI & GALLEN, 1986), pertaining to the genera *Mactra*, *Pseudocardium*, and *Spisula*, have significantly higher frequencies of complete drilling ( $P < 0.05$ ) than do the five tropical samples in Table 1 (pertaining to the genera *Mactra* and *Mactrellona*, all from Panama and Venezuela). This pattern therefore conforms with that observed in the entire pelecypod sample.

In a discussion of the various ways in which shell-bearing mollusks are subdued by predators, VERMEIJ (1987) pointed out that drilling by gastropods is an extremely slow form of predation. Unless drilling is done in habitats where the predator is safe from disturbances by physical agencies or enemies, or unless the predator is itself well adapted to withstand their onslaught, drillers are potentially at great risk while they slowly subdue and consume their prey. Rapid forms of predation, especially shell breakage and shell entry with the aid of anaesthetization or envenomation, are most highly developed among tropical predators, and may be more important causes of death for tropical than for higher-latitude pelecypods (VERMEIJ, 1978, 1987). The equatorward increase in drilling predation among turritellid gastropods therefore constitutes an odd exception to the rule that slow forms of predation decline in importance toward the tropics. It remains unclear how the turritellid pattern is to be explained. Our results on drilling in pelecypods are at least partly consistent with the idea that slow methods of predation should be more prevalent at higher latitudes.

This interpretation is supported by data on the geographical distribution of two distinct types of drilling in pelecypods, namely, side-drilling and edge-drilling. Side-drilling occurs when the hole passes through the wall of one valve; it is practiced by many muricaceans and most naticaceans (VERMEIJ, 1978, 1980a; ANSELL & MORTON, 1987). Edge-drilling occurs when the hole is made at the commissure between the valves; this is done by many muricaceans and some polinicine naticids (VERMEIJ, 1978, 1980a; KENT, 1981; ANSELL & MORTON, 1985, 1987). It is likely that edge-drilling is considerably faster than is side-drilling (ANSELL & MORTON, 1987); hence, it should be more common in the tropics. Our data suggest that this is indeed so. Only 2 of 13 cold-temperate samples (15%) (*Protothaca adamsi* at Locality 3 and *Mytilus edulis* at Locality 6) contained edge-drilled valves, but in both cases edge-drills constituted a minority (11% and 16% respectively) of the total number of complete holes. Among the

30 tropical samples in Table 2, 8 (27%) contained edge-drilled individuals; edge-drills constituted 50% or more of the total number of complete drill holes in *Chione subrugosa* from Locality 16 (100% of holes), *Protothaca mcgintyi* at Locality 16 (50%), and *Pitar albida* at Locality 10 (50%). An earlier survey in Guam also revealed high incidences of edge-drilling among pelecypods on that tropical island (VERMEIJ, 1980a).

#### Distribution and Interpretation of Incomplete Drilling

Although incomplete drilling is generally rare in the pelecypods we surveyed (Table 2), it is surprisingly common in the naticacean-drilled species from northern Japan. Indeed, contrary to expectation, our limited data failed to uncover significant differences with respect to the frequency of incomplete drilling in cold-temperate pelecypods between naticacean-drilled and muricacean-drilled samples ( $P > 0.10$ ). Among naticacean-drilled pelecypods, the 20 tropical samples in Table 2 show significantly lower frequencies of incomplete drilling than do the seven cold-temperate ones ( $P < 0.02$ ). This result is strengthened by the observation that none of the naticacean-drilled pelecypods in the samples of dead shells studied by VERMEIJ (1980a) from Guam contained incomplete drill holes.

Incomplete drill holes have usually been interpreted as unsuccessful predation attempts, but ANSELL & MORTON (1987) have shown in laboratory trials with *Venerupis japonica* eaten by various naticids that some incompletely drilled prey had nevertheless been consumed by the predator. In such cases, the prey was apparently suffocated while enveloped in the predator's foot, enabling the predator to consume the clam by way of the gap between the valves even before drilling was completed. If such cases are common, instances of successful and unsuccessful drilling cannot be distinguished consistently, so that inferences about the efficacy of drilling predators in fossil assemblages would be tenuous at best.

Analysis of the pattern of occurrence of incomplete drill holes in the sample of *Pseudocardium sachalinense* from Locality 2 suggests strongly that the incomplete holes do indeed represent unsuccessful drilling attacks. We found eight pairs and unpaired valves in which two or more holes had been drilled. In two of these, one of the holes was complete and therefore presumably lethal, whereas the others were incomplete and therefore not lethal. In the other six individuals, all holes (up to four in one pair) were incomplete. Even if one incomplete hole per individual had been lethal, 13 incomplete holes out of a total of 31 incomplete holes in the eight individuals could not have been fatal. Thus, at least 42% of the incomplete holes represent cases of unsuccessful predation. This is certainly an underestimate, because many unpaired valves with incomplete holes may originally have been joined to drilled valves that were not represented in our sample.

Besides the fact that our findings pertain to predators

Table 3

Distribution of drill holes according to shell size in *Pseudocardium sachalinense* from Locality 2 in Hokkaido.

Size class (mm)	n	C	I
20-54	21	0.33	0.14
55-64	33	0.27	0.48
65-74	44	0.07	0.09
75-84	74	0.02	0.07
85-94	37	0.05	0.08
95-104	23	0	0
105-119	18	0	0

Key: n—Number of valves. C—Frequency of complete drill holes. I—Frequency of incomplete drill holes.

and prey different from those studied by ANSELL & MORTON (1987), the studies also differ in that ours was based on collections of empty valves from the field, whereas Ansell & Morton's was carried out in the laboratory. In the latter setting, predators can attack prey without risk, and the chance that a given attack can be completed without interruption is high. Just how important such a laboratory artifact is cannot be ascertained at present. Future work comparing laboratory success rates and handling times of predators with field observations on the same species of predator and prey should help to clarify this issue.

Complete as well as incomplete holes were most frequent in the smaller valves of *Pseudocardium sachalinense* (Table 3). The peak frequency of incomplete holes was in the 55-64-mm size class, whereas that of complete holes was in the smallest size class (20-54 mm). This result cannot be taken to imply, however, that unsuccessful drilling is linked with larger prey size than is successful drilling. Individuals that were drilled incompletely were, at least in some cases, able to grow after the attack, whereas completely drilled individuals were not.

It is noteworthy that no shell of *Pseudocardium sachalinense* longer than 93 mm was marked by any drill hole. This observation suggests that clams surviving to the largest sizes were never attacked by naticids and, more interestingly, that individuals with incomplete drill holes (that is, individuals that survived attacks by naticids) did not attain large body sizes. It is therefore possible that unsuccessfully drilled individuals are weakened by the drilling ordeal, making them more susceptible to mortality than are individuals that are never attacked. Indeed, if unsuccessfully drilled individuals commonly grew well beyond the size at which they were attacked, the range of positions of incomplete holes should be considerably greater than the range of positions of complete holes, owing to the fact that the position of the hole changes as the shell of the survivor continues to grow. No such difference was found (Table 4). An alternative interpretation of the absence of large drilled individuals is that the cohort of clams represented in our sample by large adults grew to maturity at a time when naticid densities were low, whereas the

Table 4

Analysis of complete and incomplete drill holes in *Pseudocardium sachalinense* from Locality 2 in Hokkaido.

Characteristic	Complete	Incomplete
Number	18	33
Dorsoventral position on shell	0.44 ± 0.11	0.43 ± 0.12
Anteroposterior position on shell	0.45 ± 0.06	0.48 ± 0.09
Outer diameter	5.74 ± 1.25 mm	5.59 ± 0.82 mm

cohort represented by smaller individuals lived with a denser predator population. We cannot distinguish between these alternative explanations with presently available evidence.

Because the number of drill holes in our pelecypod samples is generally less than 10, we have only a few reliable estimates of the effectiveness of shells against drilling. Nevertheless, it is clear from Table 2 that several Japanese species, especially *Pseudocardium sachalinense* and *Peronidia venulosa*, have an effective armor defense against drilling, as inferred from the ratio of incomplete drill holes to the total number of holes. Comparably high values of 0.50 or higher have not previously been reported for Recent prey species, although those for Indonesian *Anadara (Tegillarca) granosa* (Linnaeus, 1758) drilled by muricaceans (effectiveness 0.41) and of *Stewartia floridana* (Say, 1822) drilled by naticaceans (effectiveness 0.35) come close (VERMEIJ, 1980b; KITCHELL *et al.*, 1981). The only species in which the effectiveness of the shell exceeds 0.50 are some thick-shelled Eocene and Miocene venerid and corbulid pelecypods (VERMEIJ, 1987).

The study of successful and unsuccessful predation makes possible the identification of prey characteristics that function to protect the prey against predation. In the sample of *Pseudocardium sachalinense* from Locality 2, however, we were unable to detect any difference in the position or size of complete and incomplete drill holes (Table 4).

The lack of difference in position between complete and incomplete holes in *Pseudocardium sachalinense* recalls the situation in a sample of *Anadara granosa* from the Indonesian island of Halmahera, in which complete and incomplete muricacean holes had a common distribution near the posterior end of the shell (VERMEIJ, 1980b). For these two species, therefore, we are unable to identify specific features of armor that serve to protect the prey against drilling despite the high overall effectiveness of armor. By contrast, incomplete holes in *Stewartia floridana* are concentrated in the distinctly thickened central portion of the valves (KITCHELL *et al.*, 1981). In the Australian limpet *Patelloida alticostata* (Angas, 1865), drilling success is dictated by how snugly the rim of the muricacean predator's aperture fits over the prey's shell; holes are more often incomplete in those parts of the shell where the fit is poor (BLACK, 1978). Incomplete holes in most fossil and living

corbulid pelecypods are concentrated in the left valve (DE CAUWER, 1985). In these clams, an internal organic shell layer seems to prevent drilling predators from completing their holes (FISCHER, 1963; LEWY & SAMTLEBEN, 1979). Finally, PALMER (1982) showed that unsuccessful attempts by muricaceans (species of *Nucella*) to drill barnacles tended to be within plates as compared to the sutures between plates. In all these cases, the differences in distribution between complete and incomplete holes point to features of armor (thick shell wall, rough or uneven surface, presence of organic layer, and limited number and length of sutures between external skeletal elements) that function effectively to prevent successful drilling.

### Concluding Remarks

Because it is so readily quantifiable in Recent as well as fossil samples of shells, drilling is perhaps the best understood form of predation on mollusks. Reasonably robust geographical and temporal patterns of successful and unsuccessful drilling are being uncovered, and estimates of the great variation at small spatial scales are becoming available. Yet, many important questions remain unanswered, and large areas of the world's marine biota remain unsurveyed with respect to drilling predation. Is edge-drilling faster than side-drilling? What accounts for the equatorward increase in drilling predation in turritellid gastropods? Is the decrease in complete and incomplete drilling in pelecypods from north-temperate latitudes to the tropics mirrored in the southern hemisphere? Do escape and lack of detection play a greater role as anti-drilling attributes toward low latitudes? With continued study, the role of drilling in the evolution of shell-bearing mollusks will become increasingly well understood.

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